


Why non-native grasses pose a critical emerging threat to biodiversity conservation, habitat connectivity and agricultural production in multifunctional rural landscapes

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Abstract

Context Landscape-scale conservation planning is key to the protection of biodiversity globally. Central to this approach is the development of multifunctional rural landscapes (MRLs) that maintain the viability of natural ecosystems and promote animal and plant dispersal alongside agricultural land uses.

Objectives We investigate evidence that non-native grasses (NNGs) in rangelands and other low-intensity agricultural systems pose a critical threat to landscape conservation initiatives in MRLs both in Australia and globally.

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Methods We first establish a simple socio-ecological model that classifies different rural landscape elements within typical MRLs based on their joint conservation and agro-economic value. We then quantify the impacts of eight Australian NNGs (*Andropogon gayanus*, *Cenchrus ciliaris*, *Eragrostis curvula*, *Hyparrhenia hirta*, *Nassella neesiana*, *Nassella trichotoma*, *Phalaris aquatica* and *Urochloa mutica*) on different landscape elements and then classify and describe the socio-ecological transformations that result at the MRL scale.

Results Our data indicate that two broad classes of NNGs exist. The first reduces both conservation and agro-economic value ('co-degrading' species) of invaded landscapes, while the second improves agro-economic value at the expense of conservation value ('trade-off' species). Crucially, however, both classes cause hardening of the landscape matrix, agricultural intensification, reduced habitat connectivity, and the loss of multi-value land use types that are vital for landscape conservation.

Conclusions NNGs drive socio-ecological transformations that pose a growing threat to landscape-scale connectivity and conservation initiatives in Australia and globally. There is an urgent need for further research into the impacts of NNGs on habitat connectivity and biodiversity within multifunctional landscapes, and the socio-ecological goals that can be achieved when landscape transformation and degradation by these species is unavoidable.

Keywords Fragmentation · Invasive grasses · Landscape conservation · Trade-off · Transformation · Connectivity

Introduction

The invasion of new habitats by non-native grasses (NNGs) can have profound implications for community dynamics, abiotic–biotic interactions, and the structure and provision of ecosystem processes and services (Strayer 2012). Some NNGs transform otherwise intact ecosystems by altering the cycling and composition of soil nutrients (Ehrenfeld 2003), soil water regimes (Holmes and Rice 1996), geomorphology and sedimentation (Eamer et al. 2013), and even fire regimes (Ehrenfeld 2010; Adie et al. 2011; MacDougall et al. 2013). Others quickly colonise and dominate disturbed systems (Firn et al. 2010; D’Antonio et al. 2011), and when coupled with anthropogenic drivers that increase their dispersal and fitness (e.g., MacDougall and Turkington 2005; MacDougall et al. 2014), have become major degraders of agricultural production systems. The role of such species as drivers of global environmental change and biodiversity decline is long recognised (Franklin et al. 2006; Friedel et al. 2011; Firn et al. 2013).

Yet, we believe the potentially serious consequences of these impacts for biodiversity conservation and habitat connectivity at the landscape scale remains poorly recognised. Impacts at this scale are critical, since biodiversity conservation has rapidly shifted in recent decades to embrace landscape-scale conservation planning which aims to support biodiversity alongside agricultural and other human land uses (Soulé et al. 2004; Worboys 2010; Doerr et al. 2011). These multifunctional (or multiple-use) rural landscapes (MRLs; Moilanen et al. 2005; Argent 2011; Polyakov et al. 2014) are ones in which native ecosystems are fragmented by other land uses or where agricultural use is extensive and mixed with biodiversity values throughout. But the fundamental tenet of landscape-scale conservation is that biodiversity can still persist in these landscapes if the relative composition of different land uses is carefully managed and if connectivity among elements in fragmented landscapes supports dispersal and other movement by a range of species (Crooks and Sanjayan 2006; Hilty et al. 2006; Smith et al. 2013).

Operationally, landscape-scale conservation initiatives involve three main activities (Whitten et al. 2011). First, additional protection is sought for areas of high conservation value. In rural landscapes these are usually areas that have not been subjected to agricultural intensification and the biotic homogenisation that accompanies the loss of specialist species in high input systems (Doxa et al. 2012; Bredemeier et al. 2015). Second, management of human-dominated areas is adjusted to create more of a balance between conservation and human needs. These multifunctional areas may be spatially planned to serve as buffers for high conservation value areas or may be part of a general mixed use ‘matrix’ (Mackey et al. 2010; Stutter et al. 2012; Smith et al. 2013). Finally, structural connectivity among areas of higher conservation value may be managed or restored to facilitate movement of species through the landscape (i.e., functional connectivity; Doerr et al. 2010). Contemporary conservation programs that include some or all of these activities include the Wildlands and Yellowstone to Yukon projects of North America (Van Der Windt and Swart 2008; Mattson et al. 2011), the Great Eastern Ranges and Gondwana Link initiatives in Australia (Whitten et al. 2011; Worboys and Pulsford 2011; Bradby 2013; Pulsford et al. 2013), and High Nature Value (HNV) farmland projects in Europe (Doxa et al. 2012; Aue et al. 2014).

There are three main reasons why we believe the power of NNGs to diminish or negate the positive work being done to generate and sustain MRLs is underappreciated. First, many NNGs challenge the pervasive environmental-agricultural weed dichotomy (viz., Stone et al. 2008), and drive changes in the biodiversity and economic value of recipient landscapes via multiple social and ecological (socio-ecological; Mansergh et al. 2008) pathways. Yet the integrated impacts of NNGs on the multifunctional nature of rural landscapes are rarely considered, with most studies focusing exclusively on either ecological or agro-economic impacts within a restricted set of landscape elements. Second, history seems to show that efforts to control NNGs have been generally ineffective at preventing either broad-scale spread or the accumulation of serious direct and indirect impacts in recipient socio-ecological systems, even when targeted early in the invasion process. Societal conflict over species value certainly impinges on the will and ability of land managers to control grasses used for

pasture improvement (Grice et al. 2012; Driscoll et al. 2014), but the same cannot be said for a growing number of less-palatable species. Third, connectivity is a core component of most landscape-scale conservation initiatives, but it has proven easier to identify, manage, and restore connections associated with woody vegetation than those associated with grasses and other ground-based vegetation (Doerr et al. 2010). Yet it is the latter that dominate many MRLs and are often most prone to invasion by NNGs.

In this paper, we combine a review of relevant literature and investigation of Australian case studies to better understand the ways that NNGs drive biodiversity decline in multifunctional rural landscapes, and implications for landscape conservation. We do this by first identifying and classifying the ways that NNGs transform different rural landscape elements, and then link these changes to the overall conservation value and functional connectivity of MRLs in general. Specifically, our approach is to:

- (1) Establish a simple, flexible model that defines MRL land use elements in terms of agro-economic and conservation values;
- (2) Use this model to articulate the goals of landscape-scale conservation initiatives conducted in MRLs globally;
- (3) Use eight Australian case studies and a brief survey of the international literature to quantify the direct and indirect mechanisms by which NNGs transform MRLs; and
- (4) Explore the losses in conservation value and functional connectivity likely to result from these changes in landscape composition and management.

We then discuss the importance and intractability of these processes in low intensity agricultural systems both in Australia and globally, and identify gaps in knowledge or capacity that influence our ability to preserve or re-connect these systems when NNGs are present.

A multifunctional rural landscape model

Many rural landscapes in Australia and other parts of the world are undergoing a multifunctional rural transition (Holmes 2006), in which biodiversity, ecological function and social amenity values are

increasingly competing against traditional productive agricultural land uses (McCarthy 2005). In these landscapes, knowledge of the joint agro-economic and conservation value of different landscape elements has become central to modern environmental decision-making (Moilanen et al. 2005; Whitten et al. 2011). It is therefore no longer possible to isolate the study of invasive or introduced species in these systems in a way that treats them as purely ecological or economic phenomena (Larson 2008), but as components of broader socio-ecological systems (Bardsley and Edwards-Jones 2007; Marshall et al. 2011) in which NNG-driven changes in anthropogenic and biophysical processes alter landscape function as a whole (Bart 2006; Bart and Simon 2013).

A model representing a socio-ecological value framework consistent with the structure of modern multifunctional rural landscapes (MRLs) is shown in Fig. 1a. For simplicity, and due to the pervasive lack of information on the impacts of most NNGs on social value and amenity, we specifically focus on core agro-economic and conservation land use values, which remain critical in virtually all lightly populated rural landscapes in Australia and elsewhere. However, we discuss the impact of the spread of amenity landscapes, in which lifestyle attributes are highly valued (Klepeis et al. 2009), on NNG control below.

In this model, landscape elements can be classified into four general types: *conservation*, *agricultural*, *degraded*, and *multi-value* (Fig. 1a). Examples of conservation landscape elements, which are cornerstones of environmental planning (*sensu* Margules and Pressey 2000), include areas of on-farm native vegetation with no or only very low intensity livestock grazing (Fig. 1a), national parks, wildlife refuges, bogs, wetlands, and significant roadside vegetation. Areas withdrawn from agricultural production under the US Conservation Reserve Program (Morefield et al. 2016) or similar set-aside schemes (e.g., Van Buskirk and Willi 2004), and through grants, tenders, or other market-based instruments (Windle and Rolfe 2008; Cooke and Moon 2015) fall into this category.

Agricultural landscape elements with lower biodiversity value include irrigated and non-irrigated crops, improved high-input non-native pastures, managed intensive rotational grazing systems, exotic and native forest industry tree plantations, woody or grassy crops for biofuel production (e.g., willow, poplar, switchgrass), and orchards. These roughly correspond to

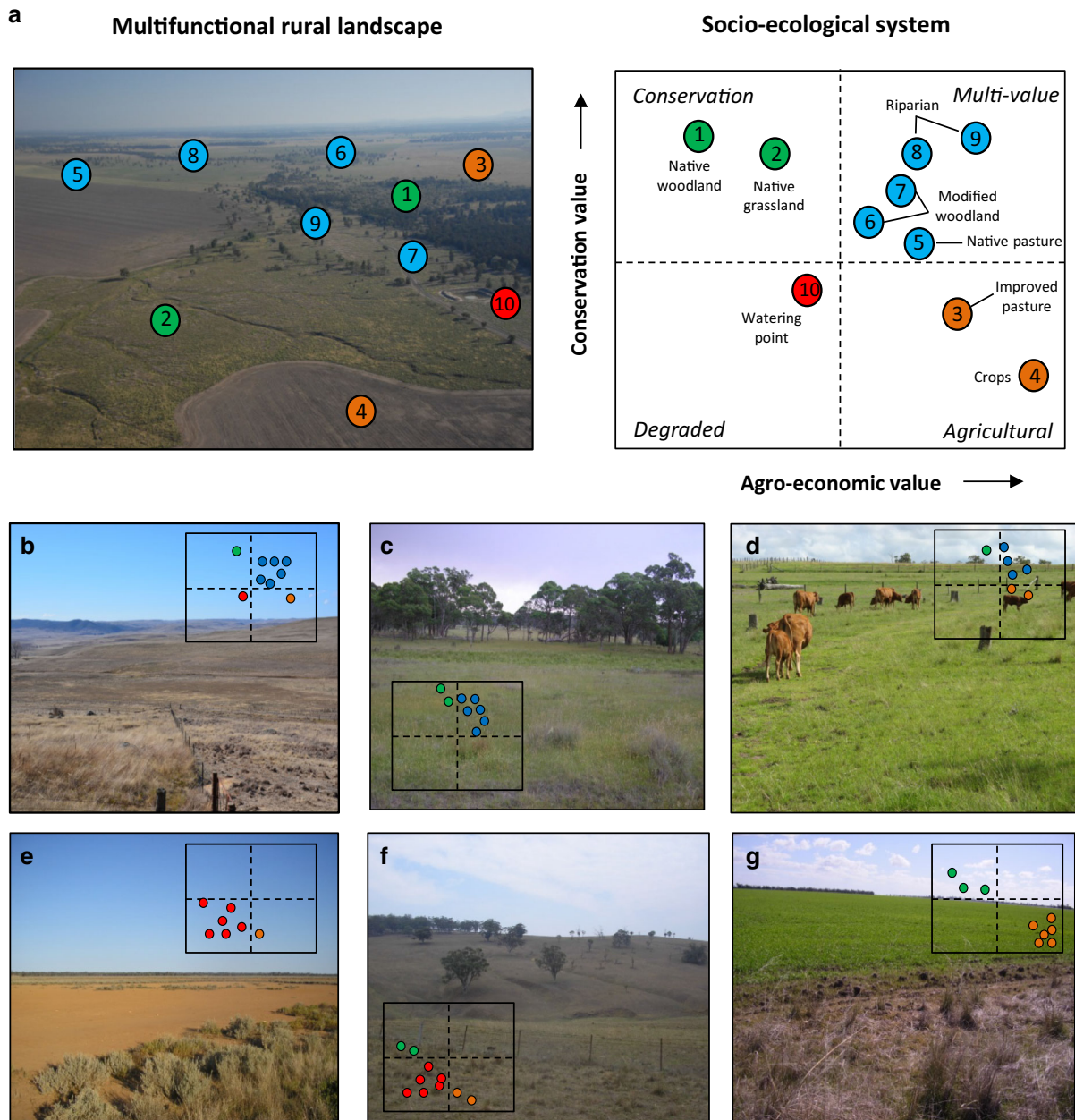


Fig. 1 A conceptual socio-ecological landscape model. **a** Multifunctional landscape in central New South Wales (NSW) containing elements that are of mainly single-value (*green* conservation; *orange* agricultural), little value (*red* degraded), or with both biodiversity and agricultural value (*blue*). Biodiverse mixed pastures (5), modified woodlands (6,7) and riparian systems (8,9) are the main multi-value areas. **b–d** Landscapes dominated by multi-value grazed native vegetation; **b** high altitude rangeland in southern NSW; **c** grassy woodland in

central eastern NSW; **d** Subtropical grassland in south-eastern Queensland. **e–g** Degraded landscapes. **e** eroded semi-arid rangeland, western NSW; **f** degraded rangeland with some remnant woody native vegetation in central NSW; **g** extensive cropping in former native grassland (foreground); western NSW. In (**g**) the landscape is polarised into discrete areas of high conservation and high agronomic value. Photos Malcolm Carnegie (**a**), R. Godfree (**b, c, e–g**), J. Stol (**d**). (Color figure online)

Holmes' (2006) productivist mode of rural land use. Globally, many productivist systems are expanding rapidly: for example, total global crop area increased by around ten million hectares per year between 2002 and 2011 (Grassini et al. 2013), while tree plantations expanded by 48% between 1990 and 2010 (Kröger 2014). Degraded elements include eroded, scalded, salinised or waterlogged soils, and overgrazed vegetation. It is estimated that land degradation hotspots cover around 29% of the global land surface area, with grasslands most severely affected (Le et al. 2014).

Of primary concern in this paper are managed, multi-value landscape elements, in which agricultural production and environmental conservation are both important goals. Although many extensive landscape elements potentially fall into this category (e.g., HNV farmland, riparian systems, silvicultural areas), our main focus here is on rangelands and pastures. These are arguably the most geographically extensive land use systems on earth (Asner et al. 2004), and perform vital socio-ecological roles throughout central and southwestern North America, southern and eastern South America, Africa, southern Europe, central Asia and Australia. Most consist of extensive, grassy or shrubby ecosystems, especially prairies, steppe, pampas, savannas, and open woodland.

In Australia, these systems are of exceptional importance. Grazed natural or modified grasslands and woodlands (Fig. 1b–d) cover 3.6 million km² (ABARE–BRS 2010), generate in excess of AU \$10 billion annual in livestock production, and contain the majority of the continental native vegetation. Historically, many have suffered significant degradation (primarily as a result of overgrazing, often combined with drought; Fig. 1e–f), and so modern projects usually focus on converting single-use agricultural or degraded production areas into connected, multi-value or conservation-oriented landscape elements. This is achieved through improved fencing and grazing management (O'Reagain et al. 2014), protection of remnant woodland and watercourses, and in severely degraded areas (Fig. 1e–g), through construction of water management features, livestock exclusion, and revegetation (Ludwig and Tongway 1996). Large multi-value areas can play a vital role in preserving landscape biodiversity (McIntyre and Hobbs 1999, Smith et al. 2013), but even when spatially restricted they can buffer remnant native vegetation and provide

supplementary habitat for native species, a process known as “matrix softening” (Haddad et al. 2014).

Following from this model, management practices that increase the conservation and agro-economic values of a given MRL simultaneously (Fig. 2a) represent particularly attractive ‘win-win’ scenarios [Fig. 2b; cf., the ‘marginalised agricultural mode’ of land use in Holmes (2006)]. For example, improved livestock management in degraded rangeland can reduce erosion, increase production, and enhance biodiversity (O'Reagain et al. 2014). Alternatively, conservation value may also be increased at little or no cost to agricultural profitability, for example by exchanging non-native for functionally similar native pasture species (‘conservation gain’; Fig. 2b). However, trade-offs (win-lose scenarios) may also be necessary to protect high quality habitat from further degradation by limiting or removing agricultural use (‘conservation trade-off’; Fig. 2b), perhaps coupled with the sacrifice of conservation value in other areas (‘agricultural trade-off’; Fig. 2b; often termed “environmental offset arrangements”; Hayes and Morrison-Saunders 2007). At the landscape level, some or all of these trajectories contribute to a transformation process (Fig. 2a) that generates landscapes compositionally capable of fulfilling multiple socio-ecological functions.

NNGs in multifunctional rural landscapes

To understand the way that NNGs transform MRLs we first need to identify the ways that they change the agro-economic and conservation value of landscape elements in which they occur. To achieve this we used a case study approach, focusing on eight representative NNG species in Australia (Table 1). Four are palatable pasture grasses (*Andropogon gayanus*, *Cenchrus ciliaris*, *Phalaris aquatica* and *Urochloa mutica*; authorities provided in Table 1), while the rest are undesirable, mainly low palatability species (*Eragrostis curvula*, *Nassella neesiana*, *Nassella trichotoma* and *Hyparrhenia hirta*). All have broad distributions in Australia (Fig. 3a–h), occur in multi-value grazed native and modified vegetation that represent a large proportion of the continental biota (Table 1; Fig. 4), and have potential ranges that span many of Australia's most important ongoing landscape-scale conservation and corridor initiatives

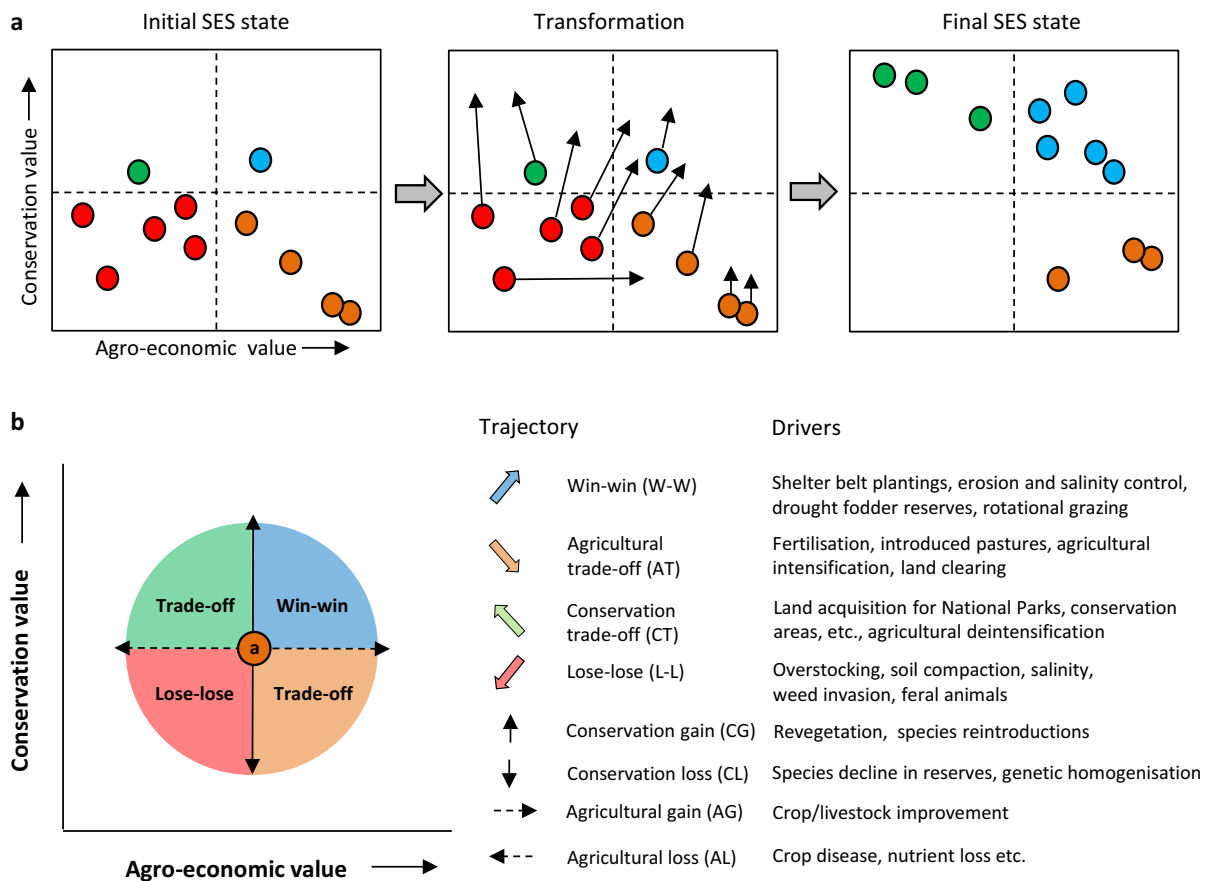


Fig. 2 Potential trajectories of socio-ecological change in multifunctional landscapes. **a** Transformation of a landscape from one dominated by single-use and degraded socio-ecological values to a higher value multi-value state with improved biodiversity conservation and connectivity. **b** Potential socio-ecological trajectories of a given landscape element (labelled **a**) fall into four main scenarios: ‘win-win’, where

conservation and agricultural value both improve; ‘lose-lose’, where both decline; ‘conservation trade-off’, where conservation value increases at the expense of agricultural value, and ‘agricultural trade-off’, where the reverse occurs. Four other restricted scenarios in which change occurs in only one value are also possible, involving agricultural gain or loss (dashed arrows) or conservation gain or loss (solid arrows)

(Fig. 4). Many are also invasive outside of Australia (e.g., Arriaga et al. 2004).

Table 2 summarises information on fourteen agro-economic (1.1–1.7) and conservation (2.1–2.7) drivers through which NNGs transform different landscape elements, and the trajectories that lead to broader landscape and socio-ecological change. These drivers, which were selected on the basis of a review of the relevant literature for each species (see Online Appendices 1–8), act either directly (1.1 and 2.1) or indirectly (1.2–1.7; 2.2–2.7) on recipient systems. Because different sources varied greatly in methodology, we simply scored the impact of each driver on

agro-economic or conservation value (see Fig. 2) as negative (–), positive (+) or neutral (0), or a combination of both (\pm or $- > +$ if a clear difference in importance). For example, *N. trichotoma* reduces agro-economic value by reducing pasture production (–score), *C. ciliaris* increases pasture value (+score), and *H. hirta* reduces pasture production and hence agro-economic value except under restricted circumstances ($- > +$ scoring). Drivers of special importance were also noted for each species; for example fire regime change is a key driver of conservation value loss associated with *A. gayanus* (–*; Table 2). Consensus socioecological trajectories were then

Table 1 Attributes of eight non-native grasses used as case study species

| Species | Origin and introduction purpose | Growth form, photosynthetic pathway, height | Habitat and range | Conservation or corridor initiatives ^a |
|---|---|--|---|---|
| <i>Andropogon gayanus</i> Kunth Gamba grass | Africa; pasture | Tussocky C4 perennial (to 4 m) | Mesic tropical savannah ecosystems, tropical pastures, roadsides; current distribution ~ 1–1.5 million ha; potential distribution 38 million ha in Northern Territory | KtC; T-A Eco-Link (NT); Ecofire*; GER* |
| <i>Cenchrus ciliaris</i> L. Buffel grass | Africa and SW Asia; pasture and erosion control | Tufted erect or spreading C4 perennial (1 m) | Tropical and subtropical arid rangelands, subhumid woodland and forests, semi-arid grassy woodlands, roadsides; widespread across inland Australia; potentially over 60% of Australian continent | KtC; T-A Eco-Link; BtB; Nature Links |
| <i>Eragrostis curvula</i> (Schrad.) Nees African lovegrass | Southern Africa; pasture and erosion control | Tufted or tussocky C4 perennial (1.5 m) | Temperate, subtropical, mediterranean and coastal native pastures, woodlands, riparian areas, roadsides, remnant native vegetation including lowland temperate grassland; potentially across most of southern and south-eastern Australia | GER; K2W; S2S; K2C; BtB; Habitat 141; GWL; MLS |
| <i>Hyparrhenia hirta</i> (L.) Stapf Coolatai grass | Africa and the Mediterranean; pasture and erosion control | Tufted or tussocky C4 perennial (1.2 m) | Native temperate, subtropical and mediterranean pastures, grasslands, grassy woodlands, roadsides, stock reserves, remnant native ecosystems, potentially tropical grasslands and savannas; vast potential distribution | GER; K2W; S2S; K2C; BtB; Habitat 141; GWL; KtC* |
| <i>Nassella neesiana</i> (Trin. & Rupr.) Barkworth Chilean needle grass | South America; accidental | Tufted or tussocky C3 perennial (1 m) | Native pastures and rangelands of temperate south-eastern Australia, remnant lowland temperate grasslands, rocky outcrops, riparian systems; potentially at least 42 million ha | GER; K2W; S2S; K2C; Habitat 141*; NLinks*; MLS* |
| <i>Nassella trichotoma</i> (Nees) Hack. ex Arechav. Serrated tussock | South America; accidental | Tussocky perennial C3 (0.6 m) | Most native pastures and rangelands of temperate south-eastern Australia, also remnant grasslands and grassy woodlands; > 1 million ha; potentially 32 million ha | GER; K2W; S2S; K2C; MLS; Habitat 141*; BtB* |
| <i>Phalaris aquatica</i> L. Phalaris | North Africa, Mediterranean, W Asia; pasture and salinity control | Tussocky C3 perennial (2 m) | Key element of most improved high-rainfall temperate and mediterranean pastures of southern and south-eastern Australia; native grasslands, grassy woodlands and forests, wetlands and riverine environments, roadsides; ~ 2.7 million ha | GER; K2B; S2S; K2C; Habitat 141; GWL; MLS |
| <i>Urochloa mutica</i> (Forsk.) T.Q.Nguyen Para grass | Probably tropical Africa; pasture and erosion control | Stoloniferous leafy C4 perennial (2 m) | Wetlands and ponded pastures and grasslands in northern and north-eastern Australia, tropical floodplains; currently 140,000 + ha, potentially most of tropical and subtropical Western Australia, Northern Territory and Queensland | KtC; T-A Eco-Link; BtB; GER; Ecofire |

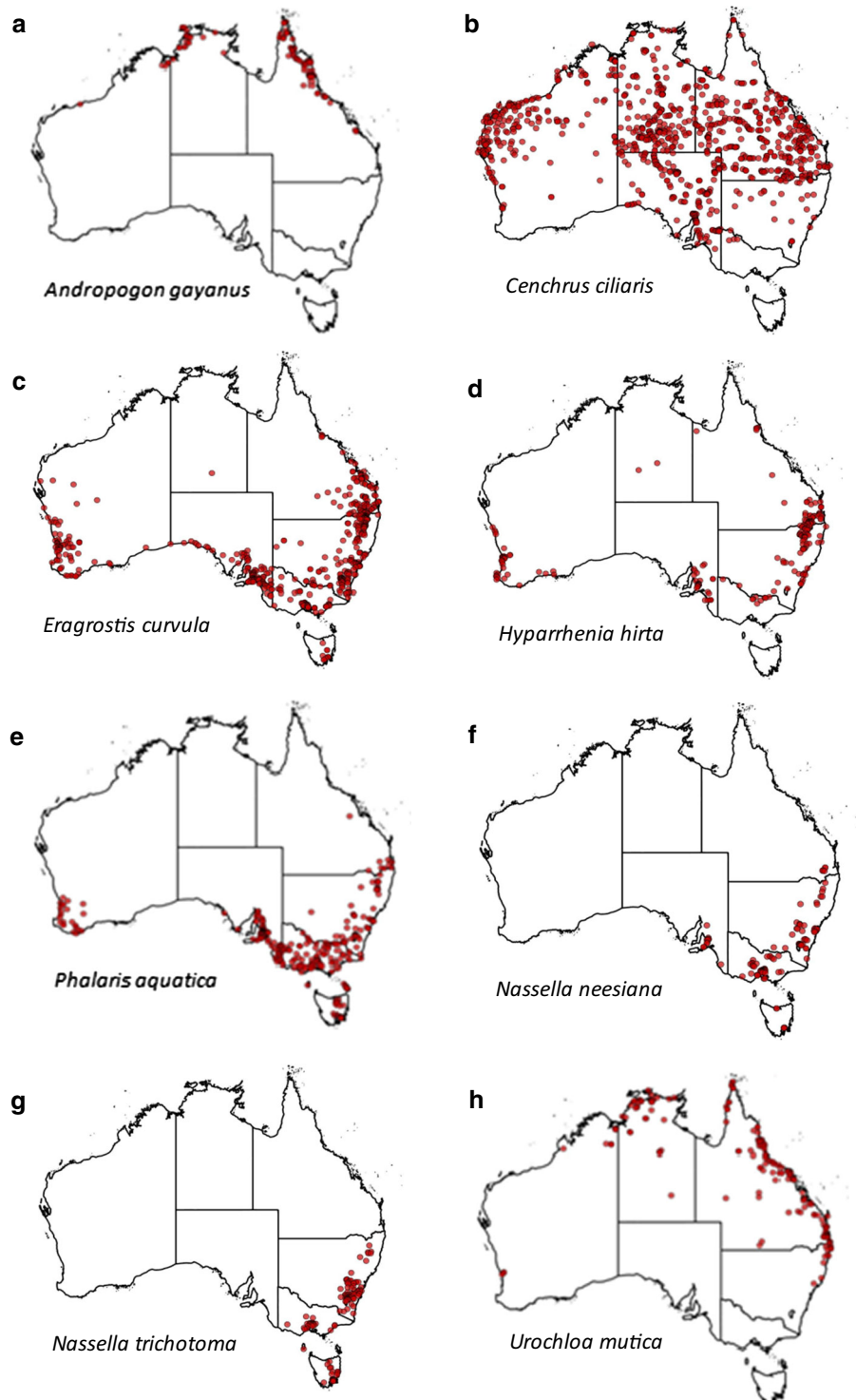
Habitat and range describe the typical habitats and potential distribution in Australia. Conservation and corridor initiatives are those that are currently in place or planned; additional details are provided in Whitten et al. 2011. Relevant references for each species are provided in Online Appendices 1–8

^a Conservation or corridor initiatives potentially affected by each grass species

KtC Kimberley to Cape initiative, T-A Eco-Link Trans-Australia Eco-Link, Ecofire Kimberley EcoFire Project, GER Great Eastern Ranges Initiative; K2W Kanangra-Boyd to Wyangala Link, K2C Kosciuszko to Coast Partnership, S2S Slopes to Summit Partnership, BtB Birdsville to Bays, Habitat 141 Ocean to Outback Project, GWL Gondwana Link, MLS Midlandscapes Project, Nlinks Nature Links (South Australia)

* Indicates conservation or corridor initiatives that are at particularly high risk

Fig. 3 Distribution of eight case study non-native grasses in Australia. Spatial data obtained from the Australia Virtual Herbarium (Council of Heads of Australasian Herbaria; <http://avh.chah.org.au/>)



constructed for each landscape element class (Fig. 1). In the following discussion we refer to only a selection of representative data to illustrate

these processes; readers are referred to Online Appendices 1–8 which contain detailed, species-specific notes and references.

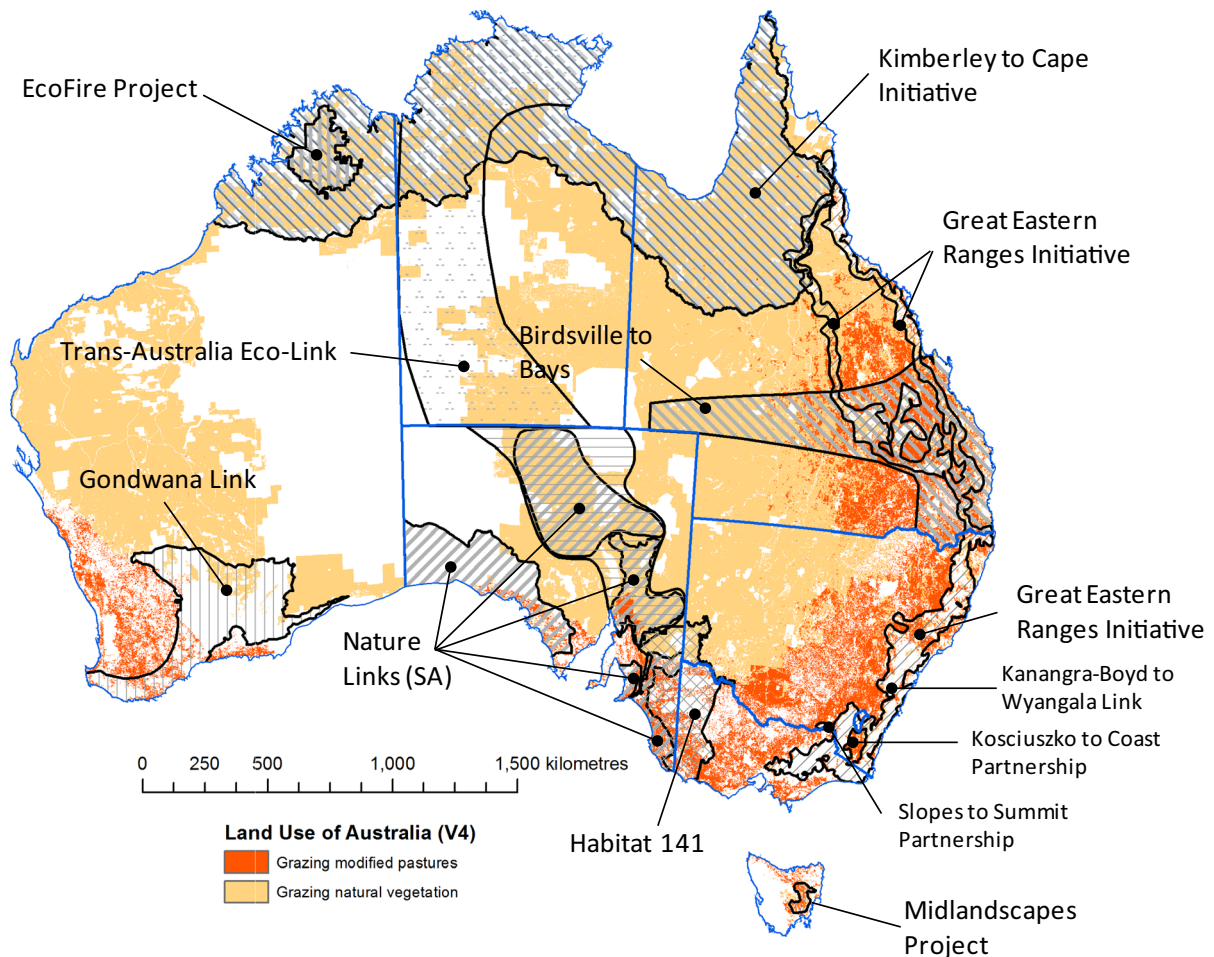


Fig. 4 Spatial extent of current and proposed landscape connectivity and corridor initiatives in Australia, along with two multi-value grazing land use types that retain significant native biodiversity. Connectivity and corridor initiatives are

from Whitten et al. (2011) while land use data are from land use of Australia 2005–06, Version 4 (ABARE–BRS 2010). ©Department of the Environment 2015

Our data indicate that the eight NNGs transform MRLs in two main ways. First, low palatability species (*N. trichotoma*, *N. neesiana*, *E. curvula* and *H. hirta*) typically drive landscape elements along lose-lose, conservation loss or agricultural loss trajectories (L-L, CL and AL; Fig. 2b), leaving the MRL in an economically and ecologically degraded state. These we term Type I or “co-degrading” transformations (Fig. 5a). In contrast, *P. aquatica*, *C. ciliaris*, *U. mutica* and *A. gayanus* generally increase agricultural production at the expense of conservation value (AT trajectories; Fig. 2b) in all but the most degraded land use types, which we call Type II or “trade-off” transformations (Fig. 5a). Landscapes altered by co-degrading transformations are likely to contain an

extensive matrix of impoverished rangeland and pasture surrounding smaller areas of intensive agriculture or remnant vegetation (Fig. 5b, c), while trade-off transformations result in more agriculturally productive landscapes of reduced conservation value (Fig. 5d, e). Both transformations represent a significant shift away from the target multifunctional state (Fig. 5a) and reverse gains made in landscape-scale conservation initiatives.

From an agro-economic perspective, co-degrading species reduce profitability by forming unproductive, often monocultural pastures (Fig. 6a; Campbell and Vere 1995; Lodge et al. 2005; Firm 2009). *Eragrostis curvula*, *H. hirta* and *N. neesiana* are occasionally viewed positively as pasture species (McLaren et al.

Table 2 Primary socio-ecological value trajectories and landscape transformation caused by each case study species

| Value | Driver(s) | Change in value and trajectory ^a | | | | | | | |
|---------------------------|---|---|---------|---------|---------|---------|--------|---------|--------|
| | | AndGay | CenCil | EraCur | HypHir | NasNee | NasTri | PhaAqu | UroMut |
| 1. Agro-economic | 1.1 Pasture production and feed value | + | + | - > + | - > + | - > + | - * | + | + |
| | 1.2 Stock injury or produce contamination | 0 | 0 | 0 | 0 | - | 0 | - | 0 |
| | 1.3 Chemical control requirement | 0 | 0 | - | - | - * | - | 0 | 0 |
| | 1.4 Stocking regime and grazing management | - | 0 | - * | - * | - | - | (-) | - |
| | 1.5 Fire management implementation or mitigation | - | 0 | - | - | (-) | 0 | 0 | 0 |
| | 1.6 Land use conversion costs | - | - | - | - | - | - | - | - |
| | 1.7 Erosion/salinity/waterlogging control | (+) | + | ± | ± | 0 | 0 | ± | ± |
| | 2.1 Direct impact on native biodiversity | - > 0 | - | - | - * | - * > + | - | - | - * |
| | 2.2 Fire regime change | - * | - * | - | - | (-) | (-) | - | - |
| | 2.3 Hydrological or nutrient regime change | - | - | - | (-) | (-) | (-) | (-) | - * |
| 2. Conservation | 2.4 Off-target chemical impacts | (-) | - | - | (-) | - * | - * | (-) | - |
| | 2.5 Land use intensification | - | - * | - * | - | - | ± | - * | - |
| | 2.6 Synergies with other invasive species | (-) | (-) | nd | nd | (-) | nd | nd | - |
| | 2.7 Restoration and rehabilitation of degraded land | (+) | ± | ± | ± | 0 | ± | ± | - |
| Trajectories ^b | Agricultural | AG > AL | AG | AL | AL | AL | AL | AG | AG |
| | Conservation | CL | CL | CL | CL | CL | CL | CL | CL |
| | Multi-value | AT > LL | AT | LL | LL | LL | LL | AT | AT |
| | Degraded | static | AT > WW | LL > AT | LL > AT | static | static | AT = WW | AT |
| | Landscape transformation type | 2 > 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 |
| | 1.1–1.7 | | | | | | | | |
| | 2.1–2.7 | | | | | | | | |
| | 1.1–1.7, 2.1–2.7 | | | | | | | | |
| | 1.7, 2.7 | | | | | | | | |
| | | | | | | | | | |

Details are provided separately for each species in Online Appendices 1–8

AG agricultural gain, AL agricultural loss, CL conservation loss, AT agricultural trade-off, LL lose-lose, WW win-win. The landscape transformation types are / co-degrading, 2 trade-off (Fig. 2)

^a Change is value is scored as: increase in agro-economic or conservation value (+), decline in value (-), no change in value (0), variable change in value (±), and no data (nd)

^b Compiled trajectories in agricultural, conservation, multi-value and degraded systems are defined in Fig. 2; only the most important are shown for degraded landscape elements

* Indicates that the driver is especially notable for the species. Scores in parentheses are probable but lack conclusive data

> Indicates that the first trajectory or transformation type is most important

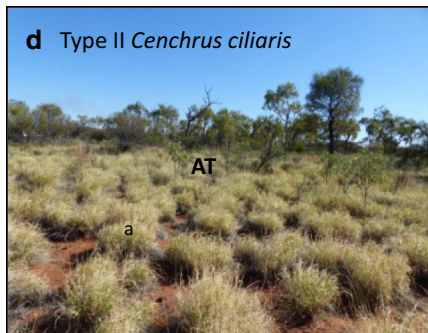
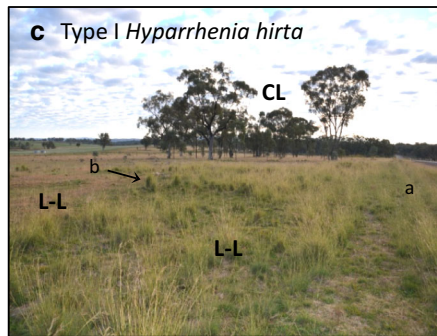
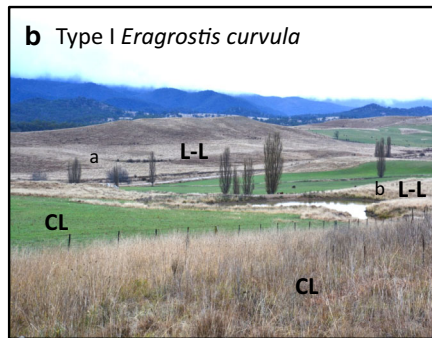
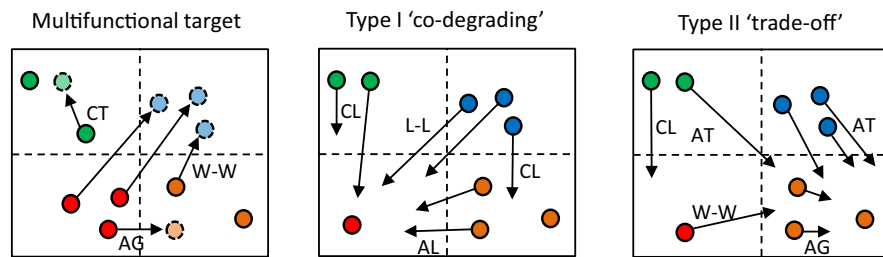
a Landscape transformation categories

Fig. 5 Transformation of Australian rural landscapes by non-native grasses. **a** Co-degrading and trade-off landscape transformations compared with the multi-functional target. **b** Invasion of the temperate pasture by *Eragrostis curvula* dominated by conservation loss and lose-lose trajectories. *Eragrostis curvula* is the light coloured grass on the lower slopes in the background (a) and near the stock watering point (b). **c** Active invasion of rangeland and remnant woodland in central NSW by *Hyparrhenia hirta*. The invasion front rapidly moves away from

the road verge (a), with individual tussocks (b) establishing in the semi-natural grassland to the left. **d** *Cenchrus ciliaris* in the arid zone of central Australia. Tussocks of *C. ciliaris* (a) can form dense monocultures. **e** Invasion of grazed savannah in northern Australia by *Andropogon gayanus*. Dense stands can develop under the native woody overstory, sometimes exceeding 3 m in height (a). Photos R. Godfree (b, c); Kerrie Bennison (d); Damien McMaster (e)

2002; McArdle et al. 2004), but the consensus is that all three species should be eradicated or controlled if possible. Indeed, maximising their palatability using fire (Fig. 6b), controlled stocking rates, mowing and/or fertiliser application (Fig. 6c; Snell et al. 2007; Osmond et al. 2008; Firn 2009; Grech et al. 2014) all incur large infrastructure and equipment costs which are often of marginal economic viability. They also

often require expensive broadacre chemical control that generates phytotoxic effects on favourable species (Osmond et al. 2008) and encourages other broadleaf weeds (Fig. 6d). Pasture renovation and conversion to rotational cropping are land use conversions (Table 2; Online Appendices 3–6) that are costly to implement and restricted to more productive areas. *Nassella neesiana* seed also directly injures livestock and

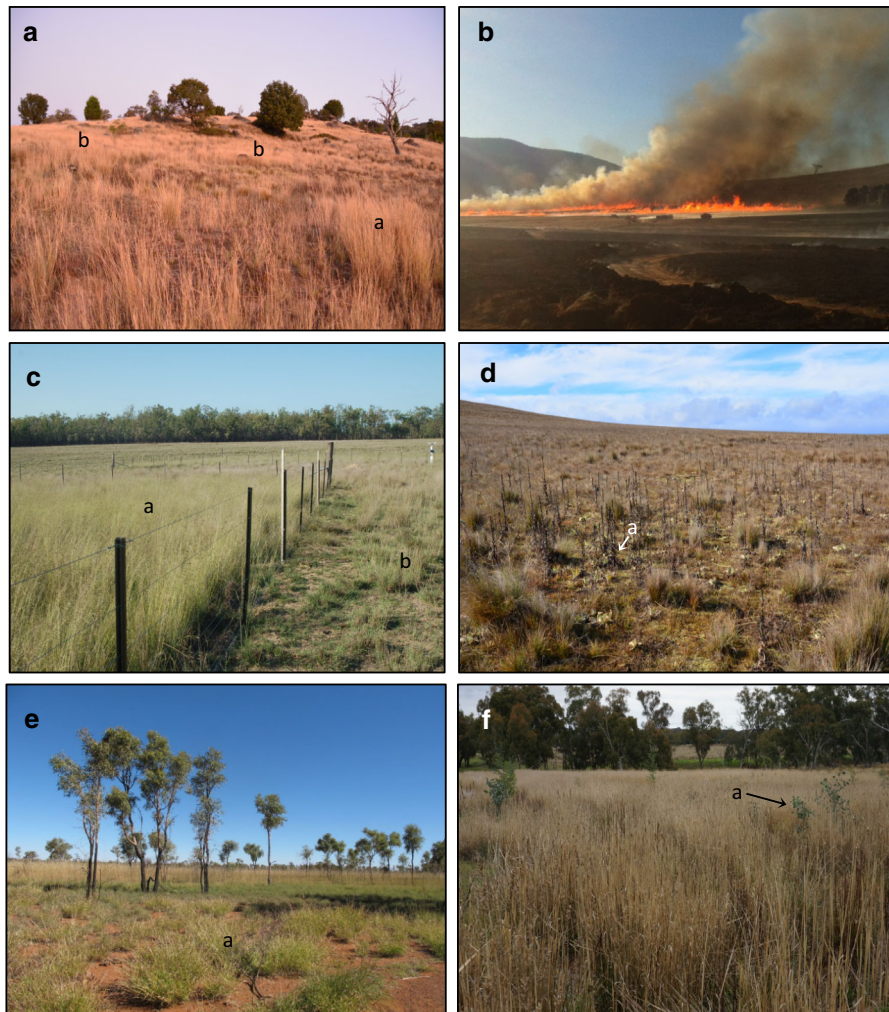


Fig. 6 Impacts of non-native grasses on landscape connectivity and conservation value. **a** *Hyparrhenia hirta* invading derived native grassland, Kanangra-Boyd to Wyangala Link (see Fig. 4). Dense clumps are shown in the foreground (a) and background (b). **b** Intense fires are characteristic of *Eragrostis curvula*—dominated grasslands, Kosciuszko to Coast Initiative. The image is of a heavily infested property being burnt to improve grazing value. Flame heights exceeded 4 m in areas of high standing *E. curvula* biomass. **c** Fertilisation and managed grazing intended to increase palatability of *E. curvula*. Ungrazed (a) and grazed (b) stands are indicated. **d** Phytotoxic effects of

herbicide use on non-target species in temperate grassland infested by *E. curvula*. The area indicated (a) has suffered from post-spray invasion by broadleaf weeds, especially *Verbascum thapsus*, following the chemical treatment of invading *E. curvula*. **e** Conversion of subtropical woodland to *Cenchrus ciliaris* pasture (a). **f** Infestation of a revegetation site in the slopes to summit partnership area by *Phalaris aquatica*. Dense stands greatly reduce the vigour of planted trees and shrubs (a). Photos R. Godfree (a, d), J. Firm (c, e), J. Stol (f), Roger Roach (b)

downgrades wool, skins, hides and carcasses (Gardener et al. 2003). While *H. hirta*, *E. curvula* and other similar species have been used to rehabilitate degraded land, they are normally detrimental in these settings because they exclude the possibility of establishing more favourable species, leaving them in a static, degraded state (Table 2).

In comparison, the trade-off species *A. gayanus*, *C. ciliaris*, *P. aquatica* and *U. mutica* have higher production value and fill significant temporal or spatial productivity gaps present in native pastures (Table 2; Tothill et al. 2008; Reed 2014). Costs associated with the establishment of these pasture species (Table 2), such as removal of pre-existing

native vegetation (Fig. 6e; Tothill et al. 2008), construction of artificial pondages (*U. mutica*; Wildin 1985), and cultivation and/or fertilization (Hill et al. 2005) are small relative to productivity gains, and so their inclusion in grazing regimes is economically attractive. They also sometimes drive agricultural gain trajectories in degraded systems and only rarely drive win–win trajectories (Fig. 5a). In some cases, notably *P. aquatica*, they may also directly hinder restoration goals (Fig. 6f). Some overlap occurs between co-degrading and trade-off species in economic value: for example, fast-growing tropical pasture grasses like *A. gayanus* can have greatly reduced economic value if not intensively managed for palatability, while the *E. curvula* cultivar Consol is moderately palatable and can add flexibility to some grazing enterprises (Johnston et al. 2005).

Impacts on landscape conservation

Our data indicate that all case study species alter landscape biodiversity on a scale that rivals that of cropping or other broadacre agricultural activities. The most obvious process is for infestations to form virtual monocultures in which other ground layer species (Ferdinands et al. 2005) are excluded from the recipient assemblage. Most NNGs grow rapidly and produce large amounts of standing biomass, which generates intense competition for soil nutrients, water and light with smaller understory or riparian plants (e.g., McArdle et al. 2004; Perna et al. 2012). This can occur on very extensive spatial scales (Table 1; Figs. 5b, d, e; 6a, c, f), leaving whole landscapes floristically impoverished, especially when other forms of disturbance, such as grazing or drought, affect the integrity of the existing native vegetation. All case study NNGs have a demonstrated capacity to directly exclude other vegetation, sometimes in the absence of significant anthropogenic disturbance; *H. hirta*, *U. mutica* and *A. gayanus* are outstanding examples (Table 2).

In most rural landscapes, however, indirect processes are probably more important drivers of native vegetation decline. Fire regime change is arguably the best example, with the dramatic ecosystem-transforming effects of the grass/fire cycle associated with *A. gayanus* threatening the long-term viability of much of the tropical savanna belt of northern Australia

(Rossiter et al. 2003; Brooks et al. 2010; Setterfield et al. 2010). There has been recent scientific debate over whether *C. ciliaris* causes the same phenomenon in semi-arid and arid ecosystems (Miller et al. 2010; Fensham et al. 2013), but the capacity for this species to modify fire regimes is also enormous (Grice 2006). Unusually intense fires have also been observed in stands of *U. mutica*, *E. curvula*, *H. hirta* and *P. aquatica*, and it is likely that the ecosystem-transforming effects of these species will increasingly be seen as a major problem for landscape conservation. Interestingly, awareness campaigns that highlight the danger of *E. curvula* fires to humans, infrastructure and livestock are currently underway in the Monaro Tablelands region of NSW.

Hydrological and edaphic change can also be a key transformative process when NNGs have seasonal resource requirements or morphological adaptations for soil water or nutrient extraction that differ from sympatric native species. This is certainly true of *A. gayanus*, which has an extended growing season compared with native grasses (Rossiter-Rachor et al. 2009) and *P. aquatica*, which increases pasture water use, reduces deep drainage (Johnston et al. 2003), but increases soil water deficits in dry times. The photosynthetic pathways of *E. curvula*, *N. neesiana* and *N. trichotoma* (Table 1) often differ significantly from the dominant grasses that they displace (e.g., Hattersley 1983), and so these species are also likely to alter soil water regimes in infested areas. Both *C. ciliaris* and *U. mutica* are major riparian weeds (Bunn et al. 1998; Marshall et al. 2012), with *U. mutica* drastically altering river sediment accumulation, streambed morphology and water discharge in infested catchments (Bunn et al. 1998). These changes have very significant indirect effects on associated riparian vegetation.

Agricultural intensification, which usually involves nutrient addition, pasture improvement, cropping, and increased grazing pressure, has a long track record of rapidly and dramatically altering rangeland and grassland composition both across Australia (Moore 1970; Dorrough et al. 2011) and globally (Tilman 1999; Sullivan et al. 2010), leaving impoverished or homogenised ecological systems. It is therefore crucial to understand that practices designed to establish, utilise or control NNGs often mimic, or even augment the broader process of agricultural intensification, and are probably the most important ways through which NNGs transform MRLs. This is most obvious with

palatable pasture species: for example, the establishment of *C. ciliaris* in subtropical areas requires the preparation of target areas by clearing, tilling and/or fertilization, often followed by a significant increase in livestock density (Fig. 6e; Tothill et al. 2008). Such practices can have a devastating impact on native vegetation and associated fauna, and currently represent a key threat to the retention of brigalow (*Acacia harpophylla*) and other woodland systems in northern Australia. In southern Australia the establishment of *P. aquatica* and other cool season perennial grasses (Reed 2014) has played a key role in reducing lowland temperate grassland to <1% of its original extent (Groves and Whalley 2002).

Less recognized, however, is that unpalatable NNGs also drive similar or greater intensification of land use. For example, integrated control is often used to manage infestations of co-degrading NNGs, including *N. neesiana* (Snell et al. 2007), *N. trichotoma* (Osmond et al. 2008) and more recently *E. curvula* and *H. hirta* (Fig. 5b). This is usually based on broadacre herbicide application followed by cultivation and establishment of non-native pastures or annual crops, effectively removing large tracts of native vegetation. In rough, sloping or infertile areas normally considered unsuitable for cropping, such practices can also drive further ecosystem degradation via erosion, soil compaction, and loss of organic matter. The fact that this process has received little attention is surprising given that the conversion of grazing lands to more intensive pasture or cropping regimes on similar scales in response to other drivers (e.g., Zhang et al. 2006) is a serious contemporary threat to biodiversity conservation in Australian rangelands and native pastures. The use of fire as a management tool to maximise the palatability of undesirable species (e.g., *H. hirta* and *E. curvula*) also clearly has the potential to accelerate broad scale biodiversity loss in Australian rangelands and pastures, especially where the removal of NNG infestations is economically or biologically impossible (e.g., Lodge et al. 1994), and where native species have low tolerance to changing fire regimes.

Finally, a range of feedback mechanisms can drive further invasion and reinforcement of ecosystem change, a process known as invasional meltdown (Simberloff and Von Holle 1999). Few studies have investigated this process in MRLs, but one example is the provision of habitat to major pest fish species by *U.*

mutica (cites in Perna et al. 2012). The impact of NNGs on fire, nutrient, water and light regimes may also precipitate self-facilitation or invasion by new species, as shown with *A. gayanus* and *C. ciliaris* (Rossiter et al. 2003; Jordan et al. 2008; Schlesinger et al. 2013). Another possible example is the planting of legumes with high phosphorous requirements to increase production of *P. aquatica* and other pasture species, leading to cascading changes in soil fertility that disadvantage native plants (Dorrough et al. 2011). Other complex interactions between factors such as competition, drought and grazing pressure can benefit unpalatable species like *N. trichotoma* (Badgery et al. 2008) and synanthropic pasture species like *C. ciliaris* (Marshall et al. 2012) at the expense of native species.

Loss of landscape connectivity

Given the capacity of NNGs to transform the structure and function of landscape elements critical to biodiversity conservation, it is surprising that the interaction between NNGs and landscape connectivity have rarely been explored. Nonetheless, there are at least three ways that NNGs are likely to erode functional connectivity for a substantial proportion of native species existing in MRLs.

First, in many MRLs the grassy understory is relatively continuous, even when associated woody vegetation has been fragmented (Mott and Groves 1994). Thus, invasion by NNGs may introduce an additional source of fragmentation, this time of the ground layer. As shown previously (Tables 1, 2), many NNGs have the capacity to form extensive monocultures which may superficially resemble native grasslands but more often vary both structurally and floristically (Daehler 2003; Brooks et al. 2010). Such habitat is likely to represent a significant barrier to movement and a reduced resource base for exploitation by native flora and fauna (e.g., Wolkovich et al. 2009). Concern has been raised that this process is occurring in the Monaro Tablelands of south-eastern NSW, where dense infestations of *Eragrostis curvula* (Fig. 5b) have developed along a >50 km long corridor between Cooma (S 36.24°, E 149.12°) and Canberra (S 35.28°, E 149.13°). The expansion of impoverished *E. curvula* grasslands is antithetical to the goals of the landscape-scale Kosciuszko to Coast (K2C) Partnership (Fig. 4), which is to protect and

reconnect forest, woodland and grassland ecosystems in this region (Godfree and Stol 2015) while maintaining rangeland grazing.

Second, NNGs in the matrix create harder boundaries between the matrix and core reserves, thus increasing edge effects and reducing effective conservation patch size. This increases the distances between those patches, which in turn reduces functional connectivity (Soons et al. 2005). Third, fragmentation is likely to be greatly exacerbated by the agricultural intensification that accompanies the conversion of pasture land to more productive use (Type II species), or efforts to control low palatability (Type I) species (see above; Figs. 5, 6). A detailed review of the plants most affected by habitat fragmentation is beyond the scope of this paper (see Henle et al. 2004), but in general they include species that require frequent regeneration from seed, lack clonal or vegetative reproduction, have low natural abundance, depend on mutualistic relationships with a small number of pollinators or seed dispersers for reproduction, lack sexual self-compatibility, and occur in restricted or specialised habitats (Davies et al. 2000; Hobbs and Yates 2003; Marvier et al. 2004; Hoffmeister et al. 2005).

Subordinate ground-based plants, especially those with naturally short dispersal distances that require fairly continuous distributions to retain functional connectivity across the landscape, are likely to be especially at risk (Murphy and Lovett-Doust 2004). In Australia, these include perennial and annual forbs that occur in the interstitial space between grass tussocks and which comprise much of the floristic diversity of grassland communities (Trémont and McIntyre 1994; Williams et al. 2006). A similar situation exists in European semi-natural grasslands, where forbs generally suffer from greater dispersal limitation than sympatric grass species (Diacon-Bolli et al. 2013), ultimately suffering genetic erosion and increased extinction risk following habitat fragmentation (Broeck et al. 2015).

The extent to which NNGs directly disrupt or provide connectivity for ground-dwelling fauna has rarely been studied, and may often be highly species-specific. Nonetheless, reptiles, amphibians, and invertebrates can depend strongly on native grassy connections, even more than on woody connections (Brown 2000; Mac Nally and Brown 2001; de Castro and Fernandez 2004), and there is abundant evidence that the fragmentation of grassy ecosystems can affect

plant-pollinator, predator-prey, host-pathogen and other critical ecological interactions (Steffan-Dewenter and Tscharntke 2002). Again, species with naturally small populations that occur in specialised floristic habitats and have restricted dietary requirements are likely to be adversely affected by fragmentation following NNG invasion due to increased demographic stochasticity, genetic decline, and impaired social function (Davies et al. 2000; Brady et al. 2011). On the other hand, at least some species appear resilient to fragmentation (Schutz and Driscoll 2008) and may even use NNGs as habitat (Richter et al. 2013). A better understanding of the characteristics of such species would greatly facilitate conservation planning in natural systems prior to NNG invasion.

As noted above, the impacts of NNG invasion on native vegetation are not restricted to the ground layer. New fire regimes (e.g., the grass-fire cycle) resulting in mortality of woody vegetation, for example, have been documented in *A. gayanus* and *C. ciliaris*, and are likely to be a factor in areas infested with the fast-growing species *H. hirta*, *E. curvula*, *U. mutica*, and probably *P. aquatica* (Table 1). The result is significant changes to connectivity of even woody vegetation and the fauna that depend on it (e.g., Law et al. 1999; Hannah et al. 2007), particularly because smaller woody connecting elements like scattered trees and corridors may be disproportionately damaged by changes in fire intensity. This is likely to be of extreme importance in modified rural landscapes where fauna depend on remnant woody cover or isolated trees for survival (Crane et al. 2014), and where community engagement in landscape conservation is motivated by concern for woodland bird or mammal species (Amos et al. 2012; Dickman 2013). The degradation of riparian systems by NNGs (e.g., Low 1997) is also likely to be a growing driver of fragmentation and loss of functional connectivity at landscape scales for many species, since such habitats play a vital role in species movement and resource provision (e.g., Bentley and Catterall 1997; Ward et al. 1999).

The management challenge

NNGs threaten the integrity of a large number of Australian landscape connectivity and conservation initiatives (Fig. 4). Yet their control is undoubtedly an

area of chronic policy failure (Graham 2013; Downey et al. 2010), and many appear to pose an exceptionally difficult, and probably unique, problem for agricultural and conservation land managers alike. Certainly, effective management strategies for NNGs on a sufficient scale remain elusive (Fensham et al. 2013), and determined efforts to control or eradicate co-degrading species like *N. neesiana* and *E. curvula* (e.g., Gardener et al. 2005; Fox et al. 2009; Coutts et al. 2013) have met with minimal success. Indeed, the situation in most areas continues to deteriorate (e.g., Godfree and Stol 2015). Even *Nassella trichotoma* (Klepeis et al. 2009), often cited as a management success story, is still locally expanding its range and requires expensive, ongoing integrated control (Osmond et al. 2008) just to maintain the status quo. Why is this so?

It appears that the intractability of many NNGs in Australia can be traced to synergisms between the morphological, genetic and ecological attributes of invasive grasses and unique socio-ecological characteristics of the Australian land mass. In short, the most problematic NNGs tend to be difficult to recognise and to be challenging or impossible to control, even on small spatial scales. These difficulties are exacerbated by the vast spatial scale of potential habitat, social and agricultural processes that facilitate spread and establishment, and the financial constraints that arise from a low rural population density (McArdle et al. 2004; Laffan 2006; Coutts et al. 2013). More recently, the ongoing expansion of amenity landscapes in Australia (Mendham et al. 2012), in which large farming properties are subdivided and sold to landowners that value lifestyle, environmental and scenic attributes over commercial interests, has increased the complexity of organizing a coordinated, effective response to invading NNGs and other broad scale environmental challenges (Klepeis et al. 2009).

While early recognition and intervention is crucial to the control of invasive species (Westbrooks et al. 2014), grasses appear to be particularly prone to oversight or misidentification, even by experienced land managers. This is particularly true when sympatric native species have similar morphological attributes (e.g., Godfree et al. 2013), or when the production of floral parts has been affected by drought or overgrazing. For example, it is common for new populations of *H. hirta*, *E. curvula*, and especially *Nassella* spp., which are morphologically similar to

Australian native *Themeda*, *Cymbopogon*, *Poa*, and *Austrostipa* species, to go unrecognised for many years. Remote sensing techniques viable for identifying grasses, while promising (Peteinatos et al. 2014), are still in only early stages of development, and not yet widely deployed. At a broader scale, many NNGs (e.g., *Themeda quadrivalvis*, *Cenchrus polystachios*, *Echinochloa polystachya*) remain outside the scope of legislation or scientific research when numbers are small and control efforts would be most effective.

From an ecological perspective, the case can also be made that Australia is especially susceptible to incursion by NNGs, which severely penalizes any lack of a coordinated detection and control effort. First, the Australian land mass is dominated by grassy ecosystems (Fig. 5), key species of which have continental or sub-continental distributions (e.g., *Themeda triandra*). The potential range of many NNGs, especially those sourced from genetically diverse populations (Godfree et al. 2013) or bred for enhanced fitness or niche breadth (e.g., Culvenor et al. 2007; Lavergne and Molofsky 2007) is correspondingly large (Fig. 3c). Most invaders also encounter few sharp topoedaphic or climatic boundaries during the initial stages of spread, and any existing barriers are often overcome by either intentional or unintentional spread. For example, seed dispersal is augmented by Australia's network of travelling stock reserves and the freight of live animals for hundreds of kilometers or more (Hogan and Phillips 2011). Roads in remote rural areas often receive little management, and the construction and intensified use of transport corridors for the growing resource and mining sector is likely to exacerbate this problem.

The invasion process is also exacerbated by the extreme variability of the Australian climate (Sivakumar et al. 2014) and the development of agricultural practices that promote the spread and establishment of synanthropic non-native species. Australian grassy ecosystems have evolved in the absence of large herbivores since the megafaunal extinctions of ~45 kyr BP, and are especially sensitive to both the removal of ground-layer vegetation by livestock during drought and to increased soil fertility. Selective grazing favours less palatable Type I species, while pulses in soil nutrient availability following drought (Austin et al. 2004) or fertilizer application tend to benefit fast-growing, nitrophilous NNGs in general. Under these disturbance regimes, which are

characteristic of low-intensity grazing practices over most of the continent, the spread of synanthropic NNGs often entails long periods of relative stasis punctuated by rapid expansion. The invasion on the Southern Tablelands of NSW by *Nassella neesiana* during and following the prolonged 2000–2009 drought is an excellent example.

From a social perspective, the development of amenity rural landscapes in Australia and elsewhere (Mendham et al. 2012), and in particular the subdivision of properties and conversion into lifestyle blocks (Klepeis et al. 2009), is also reducing the effectiveness of broad-scale NNG control programs (Coutts et al. 2013). Many people purchasing rural land have non-agricultural interests, tend to be less engaged in natural resource management and extension programs (Mendham et al. 2012), and often lack the skills necessary to identify weed species on their properties. These difficulties are exacerbated when remaining landholders, faced with heavy propagule pressure from surrounding areas, choose to simply live with NNGs. This renders the prospect of removing them from the landscape remote. Control of tradeoff-type pasture grasses like *A. gayanus* is even more challenging, since social conflict over their value makes coordination of management difficult or impossible, and many are at such advanced invasion state that broad scale control is now not seriously considered (Kean and Price 2003).

Finally, multi-trophic ecological interactions also limit effectiveness and desirability of broad-scale NNG control. For example, removal of *U. mutica* from aquatic systems can benefit other weeds such as *Hymenachne amplexicaulis* (Grice et al. 2010) and *Mimosa pigra*, or mobilise sediment which impacts downstream ecosystems. Similarly, some endangered species may depend on NNGs (e.g., the golden sun moth *Synemon plana* and *Nassella neesiana*) as a resource in otherwise degraded environments. Control of feral animals (such as the Asian water buffalo, *Bubalus bubalis* L.) may exacerbate the invasiveness of NNGs (*U. mutica*; Pettit et al. 2011). While some data exists on the multi-trophic effects of NNGs on fauna (e.g., *U. mutica*, *A. gayanus* and *C. ciliaris*), the consequences of the removal of most species, and the restoration work required to re-establish native assemblages, remains essentially guesswork. The fact that many areas now contain multiple NNGs with complementary (e.g., *U. mutica*, *H. amplexicaulis* and *E.*

polystachya) or overlapping (*E. curvula*, *H. hirta* and *N. trichotoma*) niches (Table 1; Fig. 3) further increases the complexity of their control or eradication.

Global significance

We have explored the ways that NNGs transform landscapes and degrade biodiversity using Australian case studies, and why they are difficult or impossible to manage. However, invasive grasses have a strong track record of invading rangelands and other rural systems elsewhere that have much in common, both ecologically and socially, with those in Australia (e.g., D'Antonio and Vitousek 1992; DiTomaso 2009; Zenni and Ziller 2011).

Probably the best examples of NNG transformation of MRLs come from North America. Among these, the invasion of 650 000 km² of the Great Basin by *Bromus tectorum* (cheatgrass) is most notorious, and shares many transformational features with the case studies addressed in this paper (Knapp 1996). As in Australia, advent of the livestock grazing industry in the late nineteenth century was probably instrumental in facilitating the spread of *B. tectorum* through sagebrush ecosystems, both through seed dispersal and the destruction of native vegetation (Knapp 1996). Apart from reducing grazing capacity, *B. tectorum* has the capacity to radically alter nutrient flows and seasonal water availability, and to drive the transition of vegetation into alternative system states (sensu Bowman et al. 2015) in which re-establishment of native species is impossible (Knapp 1996). The direct ecological effects of *B. tectorum* invasion are exacerbated by an increase in the frequency of fire, even at regional scales (Balch et al. 2013). Interestingly, evidence is emerging that NNGs can also reduce the size and intensity of fires, leading to different trajectories of ecological change. An example is *Festuca arundinaceae* (McGranahan et al. 2012), which, in contrast to other NNGs, generates high-moisture fuel loads; the lower rates of spread of fire in prairies containing *F. arundinaceae* ultimately result in successional change towards woodland vegetation. These and a multitude of other examples (D'Antonio and Vitousek 1992) indicate that pyrogeographical changes caused by NNGs have immense potential to

degrade the conservation value of MRLs on a global scale.

Co-degrading NNGs appear to present land managers with broadly similar challenges in MRLs worldwide, with many species originally introduced for erosion control, revegetation or pasture improvement now degrading rangelands, remnant vegetation, or both. For example, *Bothriochloa ischaemum* and other old world bluestems, which are now prevalent in Texas, have low grazing value, alter fire fuel loads, exclude native vegetation, and are difficult to impossible to control (Gabbard and Fowler 2007). As in Australia, the use of intensive grazing, fire, and fertilisation are used to enhance the productivity of *Eragrostis lehmanniana* and other low quality species in the southern USA and elsewhere (Williams and Baruch 2000). In Brazil, private companies and government bodies promote the use of *Eragrostis plana* as a pasture species, despite the fact that it is often unpalatable to cattle, and it now occupies >2 million hectares of degraded or overgrazed steppe (citations in Zenni and Ziller 2011). These processes directly displace native species and generate agricultural intensification regimes that resemble those used in eastern Australia to manage *Eragrostis curvula* (e.g., Firn 2009).

Type I pasture species also appear to pose a major challenge to landscape conservation in MRLs globally. Their adoption, usually to enhance agricultural productivity, is often linked to direct and indirect loss of high conservation-value vegetation in both agricultural and non-target rangeland or grassland habitats, with similar drivers to those identified in Australia (Table 2). For example, *Agropyron cristatum* (Christian and Wilson 1999), *Phalaris arundinaceae* (Kelllogg and Bridgham 2004) and *Festuca arundinaceae* (McGranahan et al. 2012) are serious invaders of native plant communities in North America, displacing native species and reducing biodiversity. Perhaps more importantly, however, the broad-scale clearing or modification of native vegetation to establish Type I NNG species appears to be an ongoing process worldwide. For example, the uptake of *C. ciliaris* in the Sonoran Desert region of Mexico has resulted in the clearing of extensive tracts of desert scrub, mesquite woodlands and tropical deciduous forest, with remnant areas facing ongoing invasion (Arriaga et al. 2004), even in the absence of the grass/fire cycle typical of this species (Olsson et al. 2012).

A thorough review of the relevant literature is beyond the scope of this paper, but similar case studies exist in Africa (*Arundo donax* and other riparian grasses; *Nassella* spp. and *Pennisetum setaceum*; Milton 2004); South America (*Andropogon gayanus*; *Melinis minutiflora*; Dogra et al. 2010; Zenni and Ziller 2011), New Zealand (Lamoureaux et al. 2011), and elsewhere (Dogra et al. 2010).

Conclusions and future directions

The linkages between rural multifunctionality, landscape connectivity and invasive species are in only early stages of investigation (With 2002; Haddad et al. 2014). This is surprising, given the obvious mechanistic similarity between NNGs and other agents of landscape fragmentation documented in this paper, viz. their ability to generate a hostile landscape matrix that is impermeable to native plants and animals while simultaneously degrading core conservation areas. As we have shown, impacts on biodiversity occur via two distinct modes of socio-ecological transformation, roughly aligning with palatability and agricultural utility (“trade-off” vs. “co-degrading” species). But both are inimical to the goal of generating multifunctional rural landscapes in which agricultural production and biodiversity protection are integrated (Holmes 2006) and (ideally) mutually beneficial. The destruction of associated multi-value and conservation landscape elements also poses a major threat to broad-scale habitat connectivity initiatives, particularly those dependent on market-based protection or set-aside schemes (e.g., Windle and Rolfe 2008; Cooke and Moon 2015).

The historical track record suggests that, due to a suite of social, economic and ecological constraints, the most damaging NNGs are likely to continue to spread until new equilibria are reached (Marshall et al. 2012). In many situations change is inevitable, which makes it all the more important that we come to better understand the species and landscape-traits that underpin their impacts and which strategies, if any, may reduce them in future. With this in mind, several areas of research clearly warrant further attention.

First, in situations where land managers simply have to live with NNGs, understanding their utility in multifunctional, connected landscapes will be of

immediate practical value. While eco-physiological distinctiveness is certainly a feature of NNGs, many have morphological and ecological similarities to native congeners or analogues (e.g., Godfree et al. 2013), and there may be substitutability among grasses that would allow for a basic level of connectivity and resource provision to be maintained, even in invaded landscapes. Perhaps some trade-off species have a smaller impact on conservation value than others, in which case prioritising their use could help retain multi-value landscape elements.

Second, we know little about the best way to design and implement connectivity and conservation initiatives when invasive, intractable NNGs are present in the landscape. This is especially true when co-degrading species threaten the economic viability of mixed value agricultural properties intended for inclusion in these schemes. Perhaps a combination of early identification and triage, aggressive, targeted management of priority species and populations, and funding for cross-initiative experiments into prevention and control once they are established, may succeed. How this would work for trade-off species such as *C. ciliaris* is even less clear. In some cases, it may be necessary to restrict the establishment of new landscape-scale initiatives to areas where such NNGs are not yet present.

Given the growing focus on connectivity within multifunctional rural landscapes as central to the success of continental-scale biodiversity conservation, there is a need for robust solutions to these questions as a matter of priority.

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